Insights from observations and manipulative experiments into competition between mangroves and salt marsh vegetation

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Abstract

Ecologists use multiple methods for studying interspecific competition, but different approaches may give different answers. We examined competitive interactions between *Avicennia germinans* (black mangroves) and salt marsh plants at their dynamic ecotone in Texas, USA. We compared four methods: two different methods of sampling a large (24 x 42 m) mangrove removal experiment, a transplant experiment conducted within the large experiment, and an observational study comparing sites naturally dominated by marsh or mangrove vegetation. In all of these approaches, mangroves strongly suppressed the cover and biomass of salt marsh plants. But our understanding of the strength of these interactions varied depending on the study method used, the plant species studied, and the spatial scale considered. The transplant experiment isolated the effects of competition driven only by the presence or absence of mangroves in the immediate (3x3 m plot) vicinity of the transplanted plants. In contrast, the observational study examined the combined effects of dispersal, abiotic suitability and competition as a function of the cover of mangroves at the larger plot scale. Combining the approaches in areas with levels of mangrove cover varying from 45% to 97% provided insight into how results from the local scale could be extrapolated to the landscape. In this case, although mangroves may compete strongly with neighboring marsh plants growing in their immediate vicinity, marsh plants may not be totally eradicated from sites colonized by mangroves, but instead may persist on the landscape at low densities in stressful habitats that offer a refuge from competition.

Key words: *Avicennia*, interspecific plant interaction, natural study, community composition, removal experiment

Introduction

Plant community assembly is driven by several processes, including dispersal, abiotic suitability, and species interactions (Boulangeat et al., 2012; Rand, 2000). Climate change is altering these processes, and consequently causing shifts in community composition worldwide (Huntley, 1991). One well-studied example is woody encroachment, where graminoid communities are increasingly being dominated by woody vegetation due to a variety of global changes (Lett et al., 2003; Ratajczak et al., 2012; Scholes et al., 1997). As woody vegetation increases, graminoids and forbs—and the species that depend on them—are suppressed (Lett et al., 2005)

In coastal habitats, woody encroachment is represented by the spread of mangroves into salt marshes worldwide (Saintilan et al., 2014). Plant communities in coastal wetlands, situated at the ecotone of aquatic and terrestrial ecosystems, are particularly sensitive to changes in hydrology, climate, and biotic conditions (Cherry et al., 2009; Lomnicky et al., 2019). In the U.S. Gulf Coast and the Florida Atlantic coast, the black mangrove, *Avicennia germinans*, has expanded in abundance and expanded its geographic range northward from the tropics due to warmer winters (Osland et al., 2020a), decreased severe freezing events (Cavanaugh et al., 2014; Osland et al., 2013), changes in precipitation (Osland et al., 2014b) and nutrient enrichment (Weaver et al., 2018). This species and other mangroves have expanded their ranges during periods of optimal conditions and retreated during periods of suboptimal conditions (Alongi, 2015; Montagna et al., 2011). As a result, areas near the geographic border between mangroves and marsh habitat often contain a dynamic mosaic of both habitat types expanding or contracting over time as conditions change.

Ecologists use a variety of methods to study changes in plant communities, including observations (also known as “natural experiments”) and manipulative experiments (Diamond, 1986). These methods vary in their strengths and weaknesses, and the importance of each method will vary across spatial scales, even though the main interest is centered around the same patterns of diversity and composition at the different scales (Vellend, 2010). Here, we use several methods to study competition between mangroves and salt marsh plants. Many studies have looked at how salt marsh plants affect mangrove seedlings (e.g., Guo et al., 2017; Pickens et al., 2019), because mangrove seedlings are easy to manipulate. In contrast, relatively few studies have looked at how adult mangroves, which are difficult to manipulate, affect marsh plants. Based on basic ecological theory (Keddy, 2001), we would expect adult mangroves to be competitively dominant over shorter marsh plants. Ecologists could use a variety of methods to test this hypothesis. One possible approach would be to experimentally manipulate mangrove abundance to see the effect it has on marsh plant abundance. Our experiment on Harbor Island, near Port Aransas, Texas, USA has taken this approach (Armitage et al., 2020b; Guo et al., 2017). The results of a large experiment like this one would depend not only on the competitive interactions occurring between the two types of species, but also on dispersal limitation and the abiotic suitability for species establishment (Armitage et al., 2020b; Guo et al., 2017). Another approach would be to document plant composition in large areas that naturally occur with and without mangrove cover in an observational study (Armitage et al., 2021a). The results of observations like these, because they occur on a large spatial scale, again would depend on competition, dispersal and abiotic suitability; however, dispersal limitation might be less important because the sites could represent long-term steady state conditions. The outcome of this approach, however, might be affected by pre-existing abiotic differences between areas where mangroves occurred and were absent. A third approach would be to document changes to marsh plants and mangroves caused by disturbances from natural disasters (Ferwerda et al., 2007; Osland et al., 2020b) or anthropogenic impacts (Bernardino et al., 2018; Bulmer et al., 2015; Granek et al., 2008). This is another kind of observational study, comparing across time rather than across space, with the advantage that abiotic conditions are held constant, and the disadvantage of emphasizing dispersal dynamics in a successional context. Finally, a fourth approach would be to transplant plants into areas with mangroves and areas where mangroves have been experimentally removed. By ensuring that individuals were in immediate proximity of each other and that abiotic conditions were standardized, this approach would isolate the importance of competition.

The outcome of studies on interactions between mangroves and salt marsh plants is also likely to vary depending on which marsh plant species are examined. Different marsh plant species vary in how well they can tolerate low light, reduced nutrients, and abiotic stressors (Xie et al., 2019). Because stress tolerance is often inversely related to competitive ability (Snow et al., 1984), differences in stress tolerance underlie patterns of plant zonation (Bertness, 1991; Engels et al., 2010; Pennings et al., 1992). As a result, studies comparing multiple plant species are likely to generate more insight than studies focused on a single species. Although all these approaches tell us something about species interactions, they may not all tell us exactly the same thing. The purpose of this paper is to clarify what we learn from each approach.

Finally, different types of approaches to understanding interspecific plant interactions are often carried out at different spatial scales. As a result, different outcomes could be a function of spatial scale rather than study approach per se. For example, competition is likely to occur between neighboring plants as a response to resource depletion. But, responses to species loss at the landscape scale could be due to resource depletion and a function of propagule pressure—a species cannot increase locally, even if conditions are favorable, if it is so rare on the landscape that the supply of propagules or colonists is low. Therefore, examining the role of spatial scale is fundamental to understanding why different approaches yield different results.

We worked on the Texas coast, where a number of areas have alternated between marsh and mangrove dominance over the last decades (Montagna et al., 2011). For example, during a recent period of mangrove expansion on the central Texas coast from 1990 to 2010, mangrove cover increased by 74% (Armitage et al., 2015). At the landscape scale at the time of this study, there were some areas dominated by mangroves and other areas where mangroves had not invaded and that were dominated by marsh plants. The areas dominated by mangroves sometimes had marsh plants coexisting in patches or as understory vegetation, whereas the areas dominated by marsh plants often lacked mangrove shrubs altogether (Armitage et al., 2021a).

Our overarching aim was to examine competitive effects of adult mangroves on three species of salt marsh plants in order to gain insights into how and why the community composition of salt marshes changes with differing levels of mangrove cover. To do this, we used four different methods to provide a comprehensive understanding of the interactions occurring. The first method used an observational study to document plant composition in large areas that naturally occur with and without mangrove cover. The other three methods were based around an experimental manipulation of mangrove abundance. Within this manipulation, we assessed effects of mangroves on marsh plants using a plot survey, a transect survey and a transplant experiment. All the methods are explained in greater detail below. The manipulative experiment also allowed us to examine these interactions at four different spatial scales: 3x3 m, 9x9 m and 15x15 m and 24x42 m plots. We tested three hypotheses. First, we hypothesized that competitive interactions in natural conditions would be weaker than in experimental conditions, because the communities used for the two approaches differed in terms of ambient mangrove cover. Second, we hypothesized that different marsh plant species would respond differently to mangrove competition, because different marsh species vary in their ability to tolerate abiotic stress, low light and low nutrients. Third, we hypothesized that the measured effect of competition would be a function of spatial scale, because some methods (e.g., a transplant experiment) bypass the dispersal stage, whereas others (e.g., a mangrove removal) require marsh plants to disperse into areas where mangroves are cleared.

Methods

We compared an observational study and a manipulative experiment on the central Texas coast of the Gulf of Mexico in Port Aransas, Texas. The manipulative experiment was located within the Mission-Aransas National Estuarine Research Reserve, and most of the observational study sites were located within the Mission-Aransas estuary (Appendix: Figure S1). Near Port Aransas, coastal wetlands were dominated by either the black mangrove, *Avicennia germinans,* or by a mixture of three common salt marsh plant species, *Spartina alterniflora, Batis maritima,* and *Sarcocornia* spp. (these species will be referred to by genus hereafter). Other plant species present in low abundance at the sites included: *Borrichia frutescens*, *Distichlis spicata*, *Iva frutescens*, *Lycium carolinianum*, *Monanthochloe littoralis*, *Salicornia bigelovii*, *Schoenoplectus robustus*, *Sesuvium portulacastrum*, *Spartina patens*, *Strophostyles helvola* and *Suaeda linearis*.

We compared the competitive interactions occurring between mangroves and the three common marsh species using four approaches. The first approach was an observational study, consisting of five sites dominated by marsh vegetation (named "marsh" hereafter) and five dominated by mangroves (named “mangrove” hereafter) (Appendix: Figure S2). The vegetation at these sites established naturally and was not actively planted or managed. Because of the pattern of mangrove colonization of the Texas coast, it was not possible to physically intersperse the sites representing different treatments. At each site (<20 ha), we characterized the plant community in 2015 by estimating percent cover of each species in 7-14 quadrats (1x1m) situated along a transect deployed perpendicular to the shoreline. We estimated percent cover for each plant species that was present at the sites independently, regardless of vertical overlap. Therefore, total cover of the plot could exceed 100 percent. In addition to foliar cover of each species, we also estimated percent cover of mangrove pneumatophores (aerial roots). Data are available online (Armitage et al., 2021b).

The manipulative experiment was located on Harbor Island, Port Aransas, Texas, USA (27.86° N 97.08° W). Prior to the initiation of the experiment in 2012, the area was dominated by *Avicennia*, with ~10% cover of salt marsh plants (Guo et al., 2017). Ten plots, each 24 m (parallel to the Lydia Ann Channel) x 42 m (perpendicular to the channel), were demarcated and mangroves were removed within each plot to yield one of ten cover classes of mangroves from 0% to 100% in increments of 11 percent (0%, 11%, 22%, 33%, 44%, 55%, 66%, 77%, 88%, and 100%) (Figure 1a). This manipulation mimicked mangrove dieback following a hard freeze. We divided each large plot into 3x3 m plots that either had aboveground mangrove biomass removed or left intact. This mimicked the natural patchy structure of the vegetation and also made it easier to maintain the plot mangrove cover over time. The number of plots that were removed created the appropriate plot-level mangrove cover value (e.g., 0% mangrove cover reflects all plots within the large plot removed, 55% mangrove cover reflects about half the plots within the large plot removed). This design required salt marsh vegetation to naturally colonize the areas where mangroves were removed. The clearing was completed in a stratified random checkerboard pattern, and manipulated plots were maintained every 3-4 months for the first year and annually thereafter. Within these plots, we estimated the effects of mangroves on marsh plants using three different approaches.

The first approach in the manipulation experiment was a "plot survey" conducted in 2019. We estimated vegetation cover within 3x3 m plots containing mangroves (named "mangrove" hereafter) and plots in which mangroves had been removed (named "marsh" hereafter). Plots were categorized as fringe (the front 12 m of the large plot closest to the water) and interior (back 30 m of the large plot) zones. There were six replicates of each treatment within each large plot (except for the large plots with 0 and 100 percent mangrove cover, for which only one treatment type was present), for a total of 24 plots (two vegetation treatments x two zones x six replicates) per large plot (Figure 1c). Data are available online (Pennings, 2021b).

The second approach was a "transect survey" conducted in 2019. We deployed two transects that ran from the back of each large plot to the front, with 14 contiguous plots per transect (Figure 1d). We recorded percent cover of each species in each plot as described above; data are available online (Armitage et al., 2020a). This method differed from the "plot survey" because it sampled vegetation at the very front of the large plots at the water's edge, in the middle of the large plots, and at the very back of the large plots, whereas the plot survey stratified sampling within just two zones; fringe and interior.

The third approach was a "transplant experiment". We transplanted the three most common marsh plants, *Spartina, Batis,* and *Sarcocornia*, as small clones with small (~10 x 10 x 10 cm) root balls, into each large plot in March 2013 and harvested them in November 2013. The three species were planted together in individual marsh and mangrove plots, with four replicates of each treatment per large plot spread across the fringe and interior (2 replicates in the fringe zone and 2 replicates in the interior zone) (Figure 1e). The marsh plants were not transplanted into the larger plots with 100% overall mangrove cover or 0% overall mangrove cover, because these plots did not allow a comparison between marsh and mangrove vegetation types. The 3x3 m plots were large enough that the canopies of the three transplanted species did not overlap at the end of the growing season. Thus, it is unlikely that the transplants were interacting with one another. At the end of the growing season in November 2013, the aboveground biomass of the transplants was harvested and dried to a constant mass. Data are available online (Pennings, 2021a).

We used several statistical methods to analyze the competitive interactions of mangroves on the three target marsh species. To test the first hypothesis that competitive interactions in natural conditions would be weaker than in experimental conditions, we first compared species cover (or mass for the transplant experiment) between treatment types (marsh versus mangrove) using two-sample t-tests. To evaluate the effect of the treatments on mangrove cover, we also compared mangrove cover and pneumatophore cover between treatment types. For the t-tests, the unit of replication was the 7-14 quadrats per site in the observation survey (observational study), for a total of 64 mangrove quadrats and 52 marsh quadrats. In the plot survey (manipulation experiment) the unit of replication was the 3x3 m plots from each plot, for a total of 102 mangrove plots and 105 marsh plots. The unit of replication in the transect survey (manipulation experiment) was three contiguous 1 m measurements taken within each plot in the 42 m long transects in each large plot, totaling 406 mangrove measurements and 397 marsh measurements.

The unit of replication in the transplant experiment (manipulation experiment) was the 3x3 m plots from each large plot, totaling 32 mangrove plots and 32 marsh plots.

Second, to convert abundance measures into a standard index of competition, we calculated the relative interaction intensity (RII) based on the cover (or mass) of each species of salt marsh plant in areas that represented mangrove and areas that represented marsh. We used the formula RII = $(C_{+M} – C_{-M}) / (C_{+M} + C_{-M})$, where C_{+M} is the cover/mass of salt marsh plants in the mangrove treatments (+), and C_{-M} is the cover/mass of salt marsh plants in the marsh treatments (-). This index allows marsh plant performance in the presence and absence of mangroves to scale to the total performance at each treatment. RII is a standard index of species interactions that has been used in many previous studies (Armas et al., 2004). RII values can range from -1 to 1, with negative RII values indicating competition and positive values indicating facilitation. To calculate the RII in the observational study, we haphazardly paired marsh versus mangrove sites, to give a sample size of 5 per species. To calculate the RII in the manipulation experiment, we paired the average of the marsh treatment plots with the average of the mangrove treatment plots within each of the eight, large experimental plots that had both types of treatments (thus, excluding 0% overall mangrove cover and 100% overall mangrove cover), to give a sample size of 8 per species. We compared RII values among the three plant species using ANOVA.

Third, we performed a nonmetric multidimensional scaling (NMDS) ordination as a representation of dissimilarities among plant communities, using species-specific plant cover as the response metric, based on the Bray-Curtis similarity matrix. Specifically, we compared plant communities in the marsh and mangrove treatments across the observation survey, plot survey and transect survey. Because the transplant experiment measured biomass instead of percent species cover, it was omitted from the NMDS analysis.

To test the second hypothesis that different marsh plant species would respond differently to mangrove competition, we evaluated the two-sample t-tests and RII values calculated above. We compared RII values among the three plant species using ANOVA. Additionally, we compared RII values among methods and species using a two-way ANOVA.

To test the third hypothesis that the measured effect of competition would be a function of spatial scale, we first used a two-way analysis of variance (ANOVA) for the plot survey, transect survey, and transplant experiment to compare the effects of treatment type (marsh or mangrove) and zone (fringe or interior) on the species cover or biomass. Second, we used analysis of covariance (ANCOVA) to examine the effect spatial scale, in terms of surrounding competitors, on the competitive interactions. We ran three separate ANCOVA analyses for each response variable (plant cover or biomass). In each case, the treatment type (marsh or mangrove) in the 3x3 m plot under consideration was the fixed factor, and the covariates were, in turn, 1) the number of mangrove plots in the eight 3x3 m plots immediately surrounding the plot under consideration, 2) the number of mangrove plots in the twenty-four 3x3 m plots directly surrounding the plot under consideration, and 3) the number of mangrove plots in the entire 24x42 m plot (Figure 1b). The effects of spatial scale were not analyzed at the observational study sites because the sampling design did not include measures of the vegetation surrounding each sampled plot. All statistical analyses were completed in R 4.0.3.

Results

Both the observational study and manipulation experiment effectively created distinct treatments with either marsh or mangrove dominance. Mangroves and pneumatophores were absent from plots in the marsh sites in the observational study (Figure 2ab), whereas mangroves were present at ~45% cover and pneumatophores at ~48% cover at the mangrove sites. In the plot survey within the manipulation experiment, mangrove cover and pneumatophore cover were high (>95%) in mangrove plots (Figure 3ab), but low (~1%) for mangroves and moderate (~45%) for pneumatophores in marsh plots. In the transect survey within the manipulation experiment, mangrove cover and pneumatophore cover were moderate to high (~30-75%) in mangrove plots but moderate to low (~8-13%) in marsh plots (Figure 4ab).

In most cases, marsh plant cover was greater in the marsh treatment than in the mangrove treatment in both experiment types. In the observational study, *Spartina* and *Sarcocornia* were abundant (~40-45% cover) in the marsh sites, but rare (~5-10% cover) in the mangrove sites (Figure 2ce). *Batis* did not differ in cover (~20-25%) between the marsh and mangrove sites (Figure 2d). In the plot survey within the manipulation experiment, the three marsh plants were present at moderate cover values (~10-20%) in marsh plots, but absent in mangrove plots (Figure 3c-e). In the transect survey within the manipulation experiment, the three marsh plants were present at moderate cover values (~5-15%) in marsh plots, but almost absent in mangrove plots (Figure 4c-e). Lastly, in the transplant experiment within the manipulation experiment, all three marsh plants grew several times better when planted in marsh plots (by ~3-6 times) than in the mangrove plots (Figure 5).

Comparisons of the RII across methods (Figure 6) supported the first hypothesis that the intensity of competition would vary between methods for *Batis* and *Sarcocornia*. *Batis* and *Sarcocornia* performed differently across methods (*Batis*, p=0.003; *Sarcocornia*, p=0.003), with

RII values more negative (indicating stronger competition) in the approaches within the manipulation experiment than in the observational study (Appendix: Table S1). *Spartina* performed similarly across each of the survey methods (*p*=0.16).

NMDS analysis also indicated that the composition of the plant communities differed between marsh and mangrove dominance, regardless of sampling method (Appendix: Figure S3; Table S2, PERMANOVA: observation survey, *p*=0.001; plot survey, *p*=0.001; transect survey, *p*=0.001). Within-treatment variation among samples did not differ for the observation survey (PERMDISP, *p*=0.60) but did for the plot survey (*p*=0.001) and transect survey (*p*=0.001), due to very little variation in species cover within the treatments.

Comparisons of the RII across species (Figure 6) supported the second hypothesis, that the intensity of competition would vary among species. In the observational study, *Spartina* and *Sarcocornia* both had moderately strong negative RII values (-0.75 and -0.65), indicating strong competitive interactions with mangroves. In contrast, *Batis* had almost neutral (-0.13) RII values, indicating the absence of strong interactions. In the plot survey at the manipulation experiment, all three marsh plants had highly negative RII values indicating very strong competitive interactions with mangroves, with no statistically significant differences between their responses (*p*=0.36). In the transect survey at the manipulation experiment, *Batis* and *Sarcocornia* had highly negative RII values indicating very strong competitive interactions with mangroves. *Spartina* had less extreme RII values (~-0.50), but this difference was not statistically significant (*p*=0.13). Similarly, the RII values for the three species were not significantly different in the transplant experiment (*p*=0.23). Tukey post-hoc comparisons are located in Appendix: Table S1.

The ANOVA and ANCOVA analyses supported the third hypothesis, that the measured effect of competition would be a function of spatial scale in the plot survey and transect survey, because covariates for mangrove cover at larger spatial scales were usually statistically significant, indicating that results were a function both of the treatment type (whether the immediate 3x3 m cell was dominated by mangroves or marsh plants, but also by the cover of mangroves at larger spatial scales (Appendix: Table S3; Table S4). In the plot survey, the two-way ANOVA analyzing the effects of treatment type (marsh or mangrove) and zone (fringe or interior) were consistent with the t-tests, indicating that treatment type had a significant influence on all species ($p<0.0001$), and also revealed that mangroves and pneumatophores were affected by zone within the plot (mangrove cover slightly greater in the fringe, and pneumatophore cover higher in the interior) (Pennings, 2021b). Marsh plant cover was not affected by zone. Separate ANCOVA analyses with covariates representing mangrove cover at three larger spatial scales found that all spatial scales were significantly related to cover except for *Sarcocornia* (Appendix: Table S3). For *Spartina* and *Batis*, percent cover in the marsh treatment was greater in plots with low overall mangrove cover (Appendix: Figure S3). In the case of *Sarcocornia*, none of the covariates were significant (Appendix: Table S3).

Similar results were obtained in the transect survey (Appendix: Table S4). The ANOVA results were again consistent with the t-tests, indicating that vegetation type had a significant influence on all species ($p<0.0001$), and also revealed that zone had a significant influence on all species except *Sarcocornia* ($p=0.23$). Separate ANCOVA analyses with covariates representing mangrove cover at three larger spatial scales found that the covariates were significant for each plant variable, with marsh plant cover higher in plots with low overall mangrove cover (Appendix: Figure S4, Table S4).

For the transplant experiment, the ANOVA results were again consistent with the t-tests, indicating that treatment type had a significant influence on all transplanted marsh species

(Appendix: Table S5). Plot zone did not affect the outcome for any of the plant species. Separate ANCOVA analyses with covariates representing mangrove cover at three larger spatial scales found no effects of any covariate in the transplant experiment (Appendix: Figure S5, Table S5).

Discussion

As expected, mangroves strongly suppressed the cover and biomass of salt marsh plants. But our understanding of these interactions varied depending on the study method used, the plant species studied, and the spatial scale considered. This was because the results of the different study approaches depended on different processes influencing community assembly. Because it bypassed the dispersal stage, the transplant experiment isolated the effects of competition at multiple spatial scales. In contrast, both the plot survey and transect survey within the manipulative experiment and the observational study examined the combined effects of dispersal, abiotic suitability and competition. Combining the various approaches provided insight into how results from the local scale could be extrapolated to the landscape, because outcomes depended on mangrove cover and on whether the experimental method isolated the effects of competition or also included other factors affecting community composition.

Hypothesis 1: Comparing Natural vs. Manipulative Experiment

Our first hypothesis was that the strength of competition (RII) would be weaker in the observational study than in the manipulative experiment because mangrove cover was higher at the site used for the manipulative experiment than at the sites used for the observational study. This hypothesis was supported for the two succulent species, *Batis* and *Sarcocornia*. In the observational study, mangroves did not achieve high cover in the mangrove sites, and cover of the succulents at the mangrove sites was relatively high. We did not investigate why mangroves did not achieve higher cover at these sites, but two possibilities seem likely. First, it is possible that these sites had low recruitment rates of mangroves because they were farther away from major tidal inlets that would transport mangrove propagules than were the experimental site. Second, it is possible that some patches on the landscape were too saline for mangroves, but acceptable for the succulents which are highly salt-tolerant (Debez et al., 2010; Naidoo et al., 1990). In contrast, the sites chosen for the manipulative experiment had ~90% mangrove cover. Regardless of the mechanism, because the experimental site had high mangrove cover, there were few open patches that succulents could colonize, and mangroves had a much stronger competitive effect than in the observational study. There was no difference in relative interaction intensity across the different methods for *Spartina*, which cannot colonize highly saline soils but instead was often present in a band at lower elevations than the mangroves in both the observational study and the manipulation experiment (discussed further below).

We chose our observational study sites for convenient road access and to encompass the heterogeneity of the area. We do not know whether they are representative of sites dominated by mangroves along the entire central Texas coast, but they did provide a clear contrast between sites with and without mangrove encroachment. When we set up the manipulative experiment, however, we did deliberately avoid areas with patchy mangrove cover in order to obtain a strong contrast between mangrove and marsh vegetation types. Consequently, the results of the manipulative experiment may be most relevant to areas with naturally high mangrove cover. To the extent that these areas are not representative of the Texas coast in general, this would be an example of "site-selection bias", where scientists choose to study interactions in places where they suspect that those interactions will be strongest (Mentges et al., 2021). Site-selection bias is probably common among manipulative experiments, because it is natural to pick study sites where focal species are common. In contrast, site-selection bias is often less of an issue in observational studies because of the greater spatial scale typical of observational studies (Fournier et al., 2019). In our case, where both types of experiments were deployed in the same geographic region, we were able to characterize the range of competition between mangroves and salt marsh plants on the Texas coast. Specifically, when mangroves are common, they strongly suppress salt marsh plants; however, mangroves may be sparse enough at many sites that salt marsh plants are able to coexist with them on a landscape scale.

Hypothesis 2: Comparing Marsh Plant Species

Our second hypothesis was that the three marsh species would respond differently to competition from mangroves. This hypothesis was supported, but only for the observational study, in which *Spartina* was strongly suppressed by mangroves, *Sarcocornia* moderately suppressed, and *Batis* not suppressed at all (Figure 6). As argued above, it is likely that *Batis* and to some extent *Sarcocornia*, as salt-tolerant competitive subordinates, are able to coexist with mangroves across the landscape by occupying patches that are too saline for mangrove colonization. *Spartina*, in contrast, is a flood-tolerant competitive subordinate, which is why it is often relegated to the stressful lower elevation zones (Bertness, 1991). As a result, *Spartina* can coexist with mangroves by occupying areas lower in the intertidal that are too flooded for mangroves to colonize (Naidoo et al., 1992; Xiao et al., 2010; Zhang et al., 2012); however, this strip of lower intertidal is a small fraction of the total intertidal landscape. This highlights an important bias of the observational study. In the manipulative experiment, mangroves strongly suppressed all three species of marsh plants; however, in the observational study, we observed that all three had refuges from competition in places on the landscape that were inhospitable to mangroves. Because the saline refuges were more common across the landscape than the flooded refuges, however, the observational study implied that *Spartina* was more strongly affected by competition than the two succulents. This result, however, was a function of how abiotic stress varied across the landscape, not of competition per se.

A general, although perhaps obvious, lesson from this comparison is that studies of a single species may not be representative of the community as a whole. To the extent possible, studies of mangrove encroachment—or the spread of any new species in any community—should examine effects on as many species in the community as possible in order to understand the range of competitive interactions.

Hypothesis 3: Spatial Scale

Our third hypothesis was that spatial scale would influence our measures of competition between mangroves and marsh vegetation. We explored this in the manipulation experiment by testing three covariates in three separate analyses: number of mangrove plots surrounding the 3x3 m plot in question in the 24x42 m large plots, the number of mangrove plots in the twenty-four immediate surrounding plots, and the number of mangrove plots in the eight immediate surrounding plots. We did not run a single analysis with all three covariates because they were highly correlated with each other, given that each scale included the smaller one. For the plot survey and transect survey, the analysis revealed that each of the covariates was important for predicting cover of *Spartina* and *Batis*. In other words, for these two species, competition was not solely localized at the 3x3 m plot, but rather it was a function of mangrove cover at larger spatial scales as well. Results for *Sarcocornia* cover were ambiguous, perhaps because it was the rarest of these three marsh plants at the site: the covariates were important in the transect survey but not in the plot survey. In contrast, biomass of the transplanted plants was unaffected by any of the covariates, indicating that competition in this case was solely between immediate neighbors, and not affected by plants in surrounding stands.

The most likely explanation for these different results is that the results of the plot survey and transect survey were affected both by colonization in the early dispersal life stage and competition for various resources in multiple life stages. In contrast, results of the transplant experiment were affected only by competition for various resources in the later life stages, since the transplant methodology by definition ensured that local plots were colonized. Viewed this way, the difference between the methods is consistent with ecological theory. Interspecific plant interactions should primarily occur between immediate neighbors, because plants deplete resources and experience abiotic conditions at local scales (Kneitel et al., 2004). In contrast, plot-level spatial scales influence community composition primarily by affecting the initial compositional variation among communities and dispersal (Cadotte, 2006). In the case of our manipulation experiment, marsh plants needed to naturally colonize the mangrove removal plots in order to be counted in the plot and transect surveys. They were more successful in doing so in low mangrove cover plots (Appendix: Figure S3; Figure S4), likely because they spread clonally by ramets growing from adjacent marsh plots, or from propagules produced by plants in nearby marsh plots. Marsh cover was higher in plots with low mangrove cover, leading to a greater supply of potential colonists to other marsh plots. In contrast, once marsh plants were successfully established, as was ensured in the transplant experiment, competition was solely among immediate neighbors. More generally, studies of competition that rely on removing one species and observing how another responds may commonly underestimate the strength of competition if the focal species is dispersal limited. As this discussion has shown, it is not the case that one methodology is superior to another; rather, the different methods have different strengths and weaknesses, and test slightly different questions. In some cases, one method may align perfectly with the specific questions being asked in a particular study. In other cases, a combination of methods will provide more insight than any one method alone.

Conclusion

Mangroves are expanding in many areas as climate changes, with the result that intertidal vegetation changes dramatically from low-stature, marsh plants to taller, woody mangroves. This shift is ongoing in many areas along the northern US Gulf Coast (Gabler et al., 2017), specifically in areas across Texas (Comeaux et al., 2012), Louisiana (Osland et al., 2014a), western Florida (Osland et al., 2012), and also on the Atlantic coast in eastern Florida (Cavanaugh et al., 2014). Mangrove expansion is also occurring on the coast of China (Peng et al., 2018; Zhang et al., 2012), Peru, the Pacific Coast of Mexico, South Africa (Saintilan et al., 2014), and southeast Australia (Coleman et al., 2021). Our manipulative experiment and observational study complemented each other to identify different processes influencing this vegetation shift. In particular, although mangroves may compete strongly with marsh plants at the local scale, marsh plants may not be totally eradicated from sites colonized by mangroves, but instead may persist on the landscape at low densities in stressful habitats that offer a refuge from competition. One possible caveat is that our results were obtained from the western Gulf of Mexico, where mangroves are stunted by abiotic stress (Osland et al., 2018). In mangrove-marsh ecotones where mangroves attain greater heights (e.g., the Atlantic Coast of Florida), mangrove competitive dominance is likely to be enhanced but not complete (Dontis et al., 2020; Peterson et al., 2012). We recommend that future studies of interactions between mangroves and salt marsh plants in other locations—and of woody encroachment in general—use both observational studies and manipulative experimental approaches in order to gain a more nuanced understanding of the nature of these interactions.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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Figure Legends

Figure 1. a) Layout of the manipulation experiment. Pictured are the ten large plots, each 24 m (parallel to the Lydia Ann shipping channel) x 42 m (perpendicular to the shipping channel), that were demarcated and mangroves removed within each smaller plot to cover classes from 0% to 100% in increments of 11 percent (0%, 11%, 22%, 33%, 44%, 55%, 66%, 77%, 88%, and 100%). Plots are outlined in dotted-white, and percent overall coverage is marked next to the plots. Photo by Anna Armitage. b) Design of the ANCOVA analyses. Pictured is a visual example of the layout of a plot (55%) to represent how the spatial factors were configured. The 3x3 m marsh or mangrove plots, in this case a marsh plot shaded in white, are the focal treatment type treated as a fixed factor. The three covariates were: 1) Number of mangrove plots in the eight 3x3 m plots immediately surrounding the plot under consideration; outlined in yellow (in this case there are 5), 2) Number of mangrove plots in the twenty-four 3x3 m plots immediately surrounding the plot under consideration; those outlined in blue plus those outlined in yellow (in this case there are 14) and 3) the number of mangrove plots in the entire 24x42 m plot; area outlined in white (in this case there are 62; exact locations not shown to avoid clutter). This image depicts one 3x3 m plot as an example, but the analysis was performed for each of the 3x3 m plots that were monitored using each survey method. The debris in and at the front of the plot is from the aftermath of Hurricane Harvey in 2017; photo taken shortly after. Photo by Rachel Glazner, permission granted from Anna Armitage. c) Study design of the plot survey. All 24 replicates per plot are not shown as the picture denotes the general layout of the selected plots. d) Study design of the transect survey. e) Study design of the transplant experiment. Locations of the selected plots are pictured as an example, however locations varied for each plot.

Figure 2. Observational Study: Effect of treatment type (i.e., marsh = marsh-dominated sites, mangrove = mangrove-dominated sites) on percent species cover of mangroves and the three most common marsh plant species. Error bars indicate standard error of the mean, and *t*-value(df) and *p*-value represent results from a two-sample unpaired t-test.

Figure 3. Manipulative Experiment: (Plot survey) Effect of treatment type (i.e., marsh = mangrove removed plots, mangrove = mangrove intact plots) on percent species cover of mangroves and the three most common marsh plant species. Error bars indicate standard error of the mean, and *t*-value(df) and *p*-value represent results from a two-sample unpaired t-test.

Figure 4. Manipulative Experiment: (Transect survey) Effect of treatment type (i.e., marsh = mangrove removed plots, mangrove = mangrove intact plots) on percent species cover of mangroves and the three most common marsh species. Error bars indicate standard error of the mean, and *t*-value(df) and *p*-value represent results from a two-sample unpaired t-test.

Figure 5. Manipulative Experiment: (Transplant experiment) Effect of treatment type (i.e., marsh = mangrove removed plots, mangrove = mangrove intact plots) on harvested aboveground biomass (grams) of the three transplanted marsh species. Error bars indicate standard error of the mean, and *t*-value(df) and *p*-value represent results from a two-sample unpaired t-test.

Figure 6. Comparisons of the relative interaction intensity (RII) for each of the three common marsh species across the four study approaches. Negative values represent competition with mangroves whereas positive values represent facilitation by mangroves. Error bars indicate

standard error of the mean. The *p*-values in the title of each panel represent a comparison of methods within each species using ANOVA to test the first hypothesis, that the observational survey would show less extreme competitive interactions than the methods conducted at the manipulation experiment; the *p*-values within the first panel in each method's column represent comparisons of species within each method using ANOVA to test the second hypothesis, that the three marsh species would respond differently to mangrove competition. Complete ANOVA tables are provided in the supplementary materials (Appendix: Table S1).

Figure 7. NMDS comparing between treatment types for each sampling method. Multivariate composition of communities within marsh (light-shaded polygon with white squares) or mangrove (dark-shaded polygon with grey circles) treatments in a) the observation survey (observational study), b) plot survey (manipulative experiment), and c) transect survey (manipulative experiment). The nonmetric multidimensional scaling (NMDS) ordination is a representation of dissimilarities among treatments based on plant abundance using the Bray-Curtis similarity matrix, square root transformed. 2D stress values are shown.

Figure 1

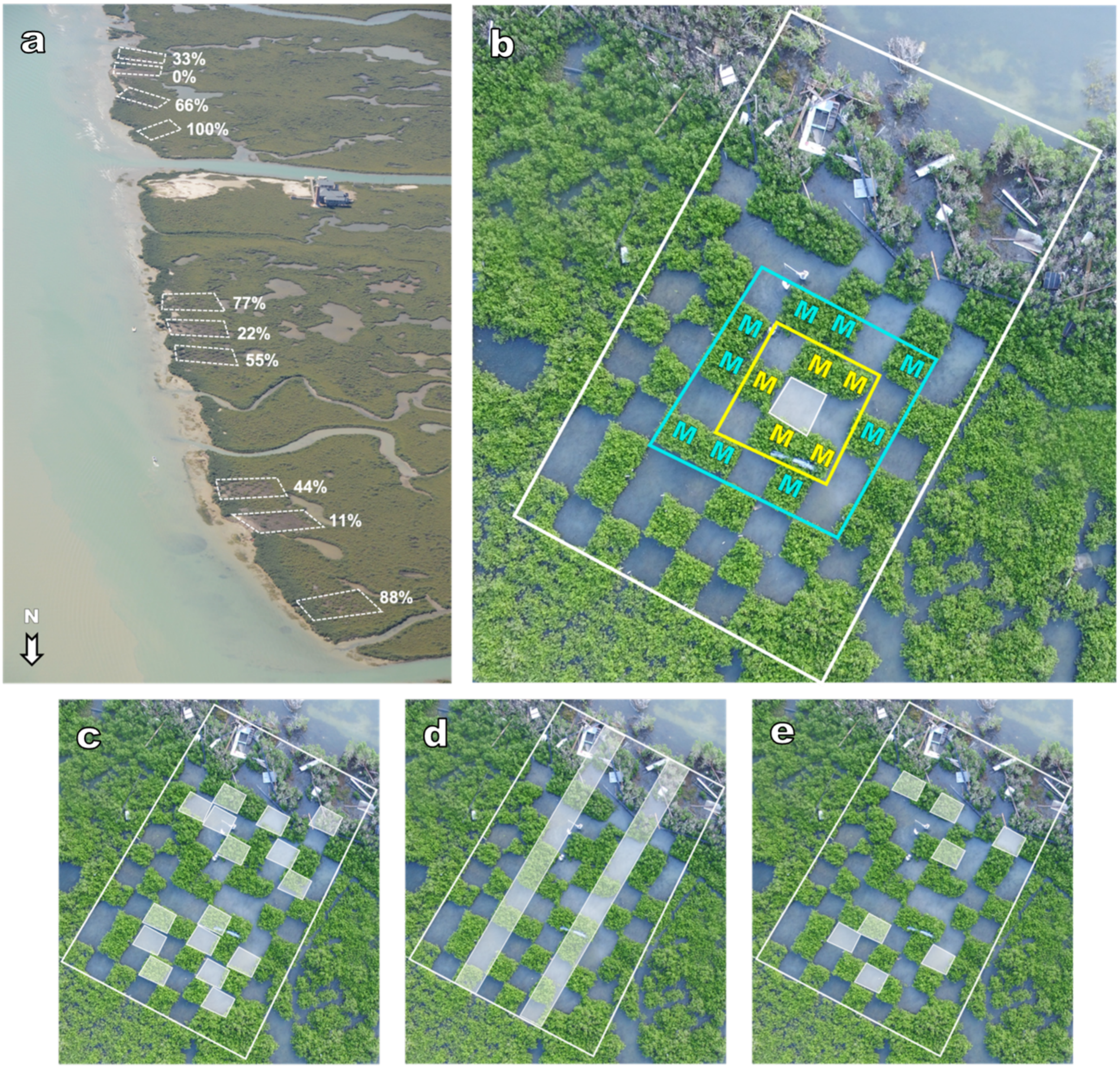


Figure 2

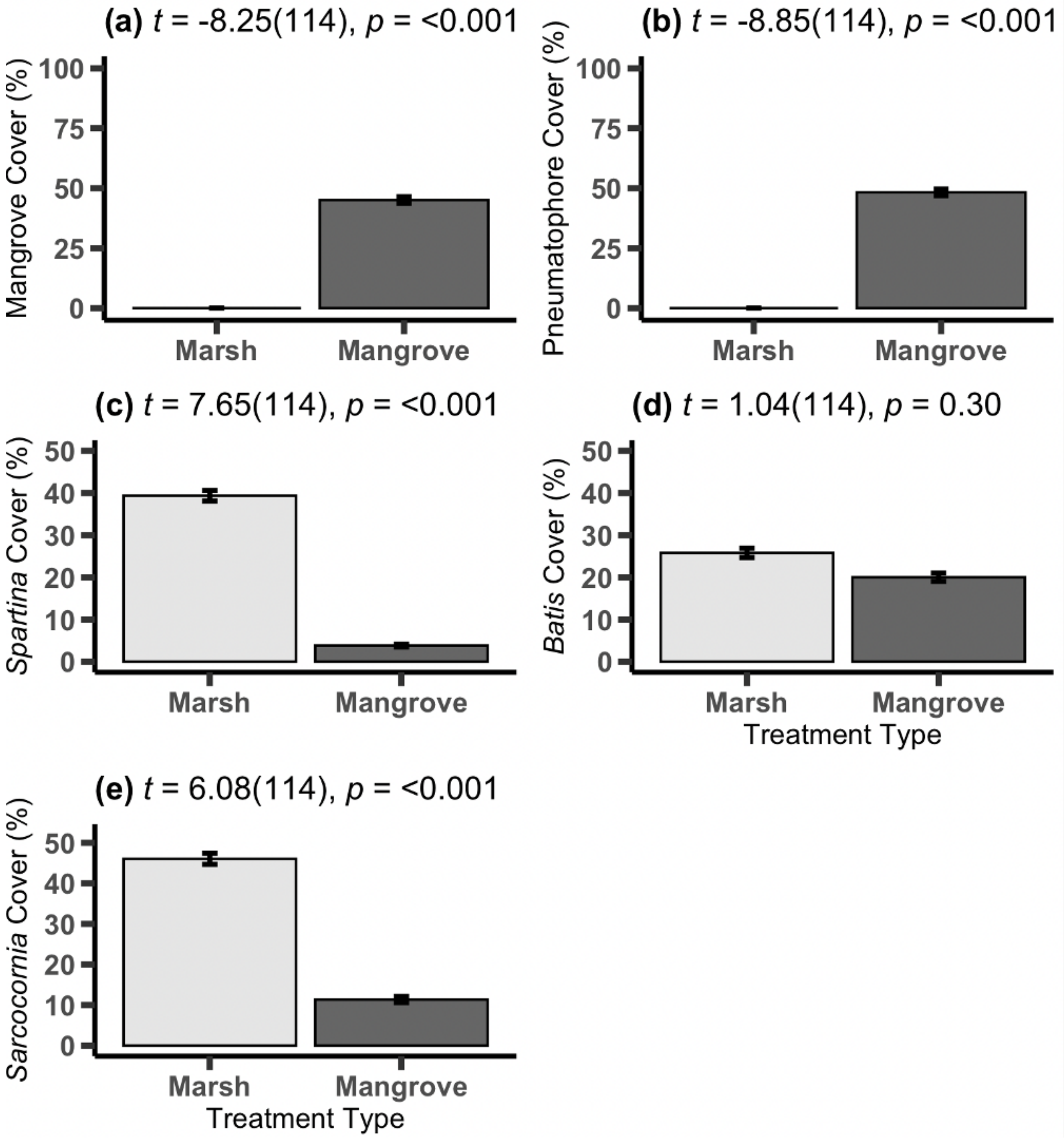
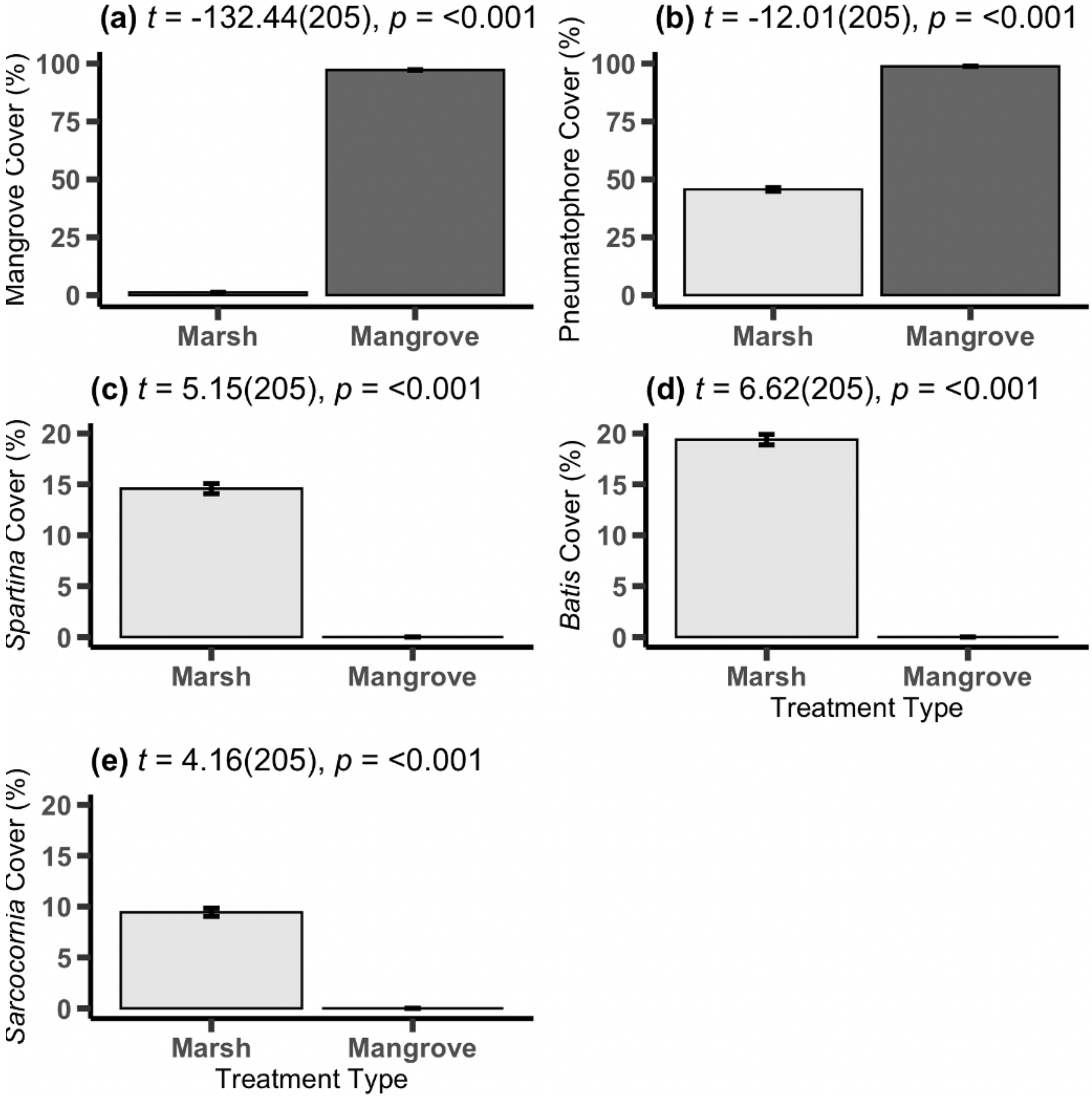

(a) t = -8.25(114), p = <0.001
Mangrove Cover (%)
100
75
50
25
0
Marsh
Mangrove
(b) t = -8.85(114), p = <0.001
Pneumatophore Cover (%)
100
75
50
25
0
Marsh
Mangrove
(c) t = 7.65(114), p = <0.001
Spartina Cover (%)
50
40
30
20
10
0
Marsh
Mangrove
(d) t = 1.04(114), p = 0.30
Batis Cover (%)
50
40
30
20
10
0
Marsh
Mangrove
Treatment Type
(e) t = 6.08(114), p = <0.001
Sarcocornia Cover (%)
50
40
30
20
10
0
Marsh
Mangrove
Treatment Type

Figure 3



(a) t = -132.44(205), p = <0.001
Mangrove Cover (%)
100
75
50
25
0
Marsh
Mangrove
(b) t = -12.01(205), p = <0.001
Pneumatophore Cover (%)
100
75
50
25
0
Marsh
Mangrove
(c) t = 5.15(205), p = <0.001
Spartina Cover (%)
20
15
10
5
0
Marsh
Mangrove
(d) t = 6.62(205), p = <0.001
Batis Cover (%)
20
15
10
5
0
Marsh
Mangrove
Treatment Type
(e) t = 4.16(205), p = <0.001
Sarcocornia Cover (%)
20
15
10
5
0
Marsh
Mangrove
Treatment Type

Figure 4

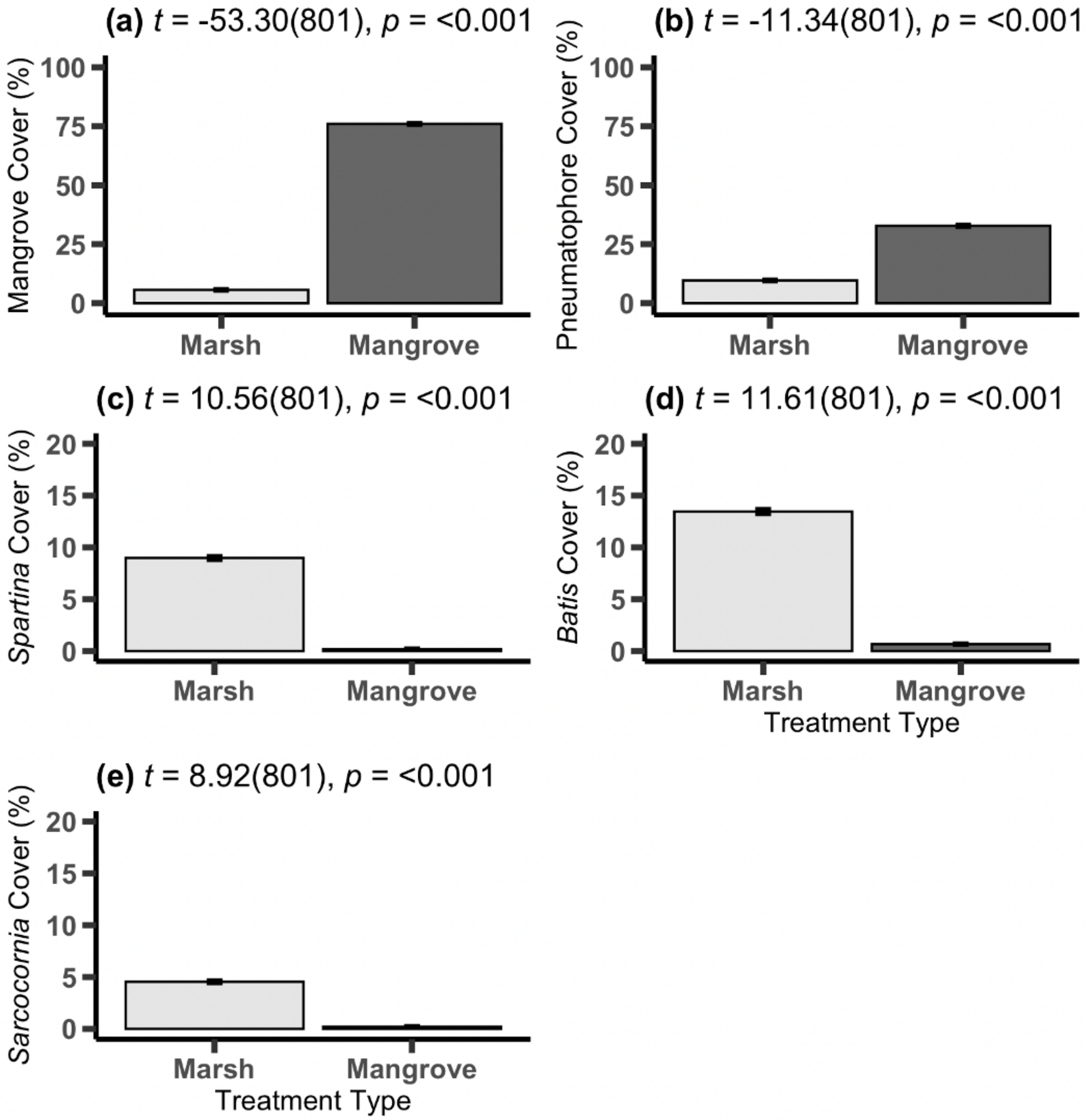

(a) t = -53.30(801), p = <0.001
Mangrove Cover (%)
100
75
50
25
0
Marsh
Mangrove
(b) t = -11.34(801), p = <0.001
Pneumatophore Cover (%)
100
75
50
25
0
Marsh
Mangrove
(c) t = 10.56(801), p = <0.001
Spartina Cover (%)
20
15
10
5
0
Marsh
Mangrove
(d) t = 11.61(801), p = <0.001
Batis Cover (%)
20
15
10
5
0
Marsh
Mangrove
Treatment Type
(e) t = 8.92(801), p = <0.001
Sarcocornia Cover (%)
20
15
10
5
0
Marsh
Mangrove
Treatment Type

Figure 5

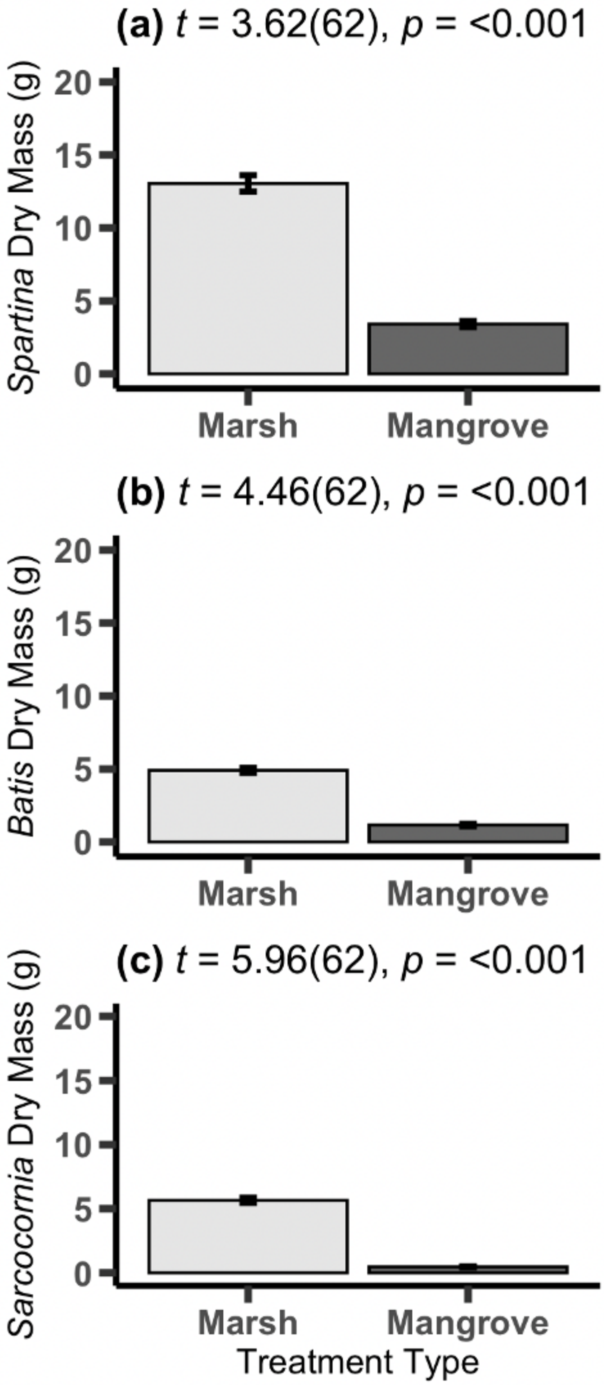
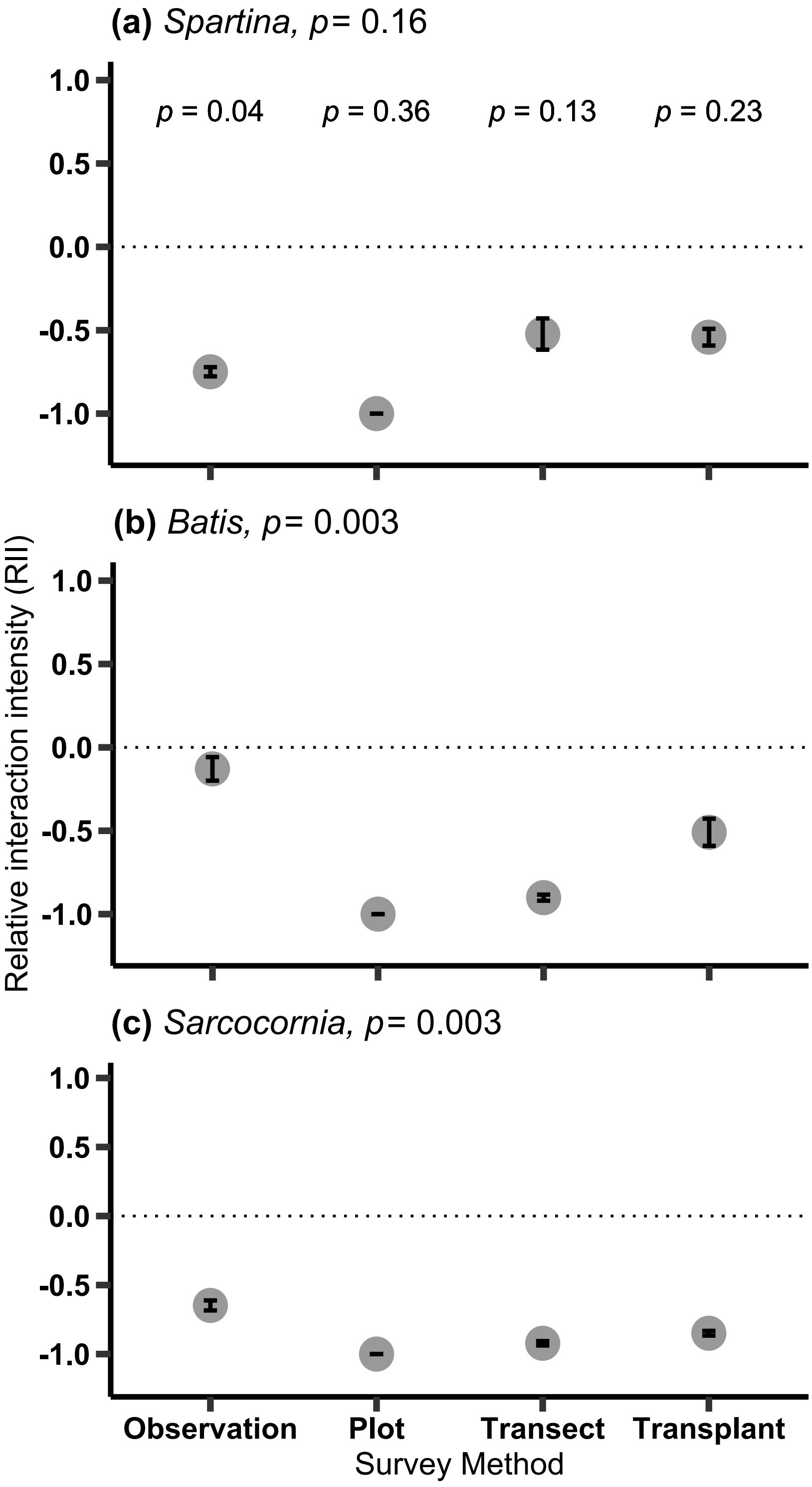
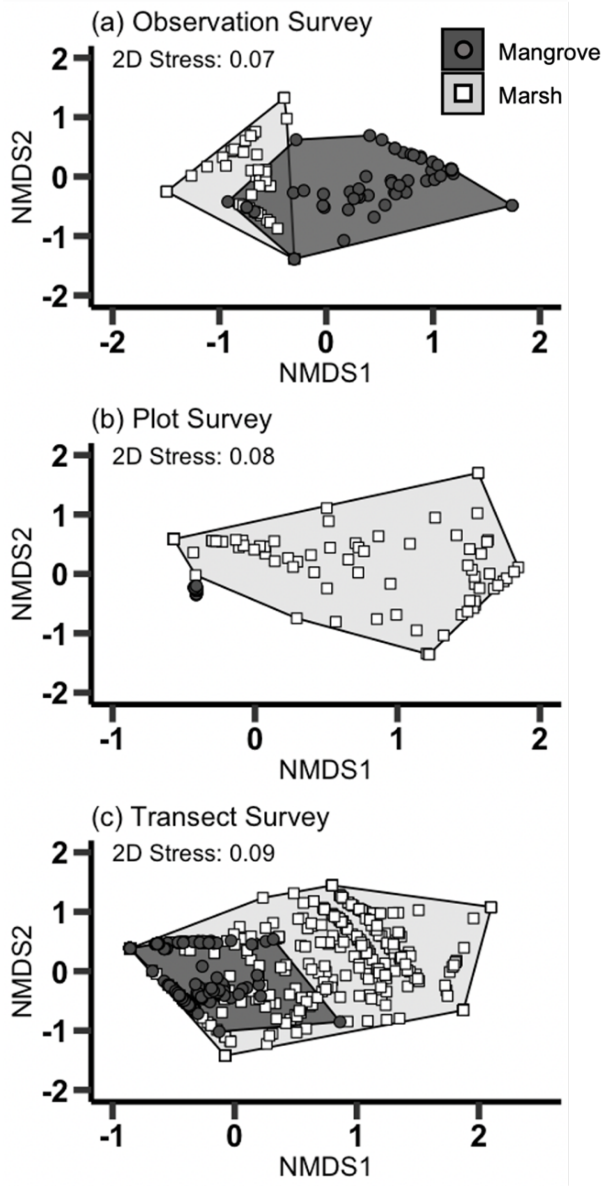

(a) t = 3.62(62), p = <0.001
Spartina Dry Mass (g)
20
15
10
5
0
Marsh
Mangrove
(b) t = 4.46(62), p = <0.001
Batis Dry Mass (g)
20
15
10
5
0
Marsh
Mangrove
(c) t = 5.96(62), p = <0.001
Sarcocornia Dry Mass (g)
20
15
10
5
0
Marsh
Mangrove
Treatment Type

Figure 6



(a) Spartina, p= 0.16
p = 0.04
p = 0.36
p = 0.13
p = 0.23
(b) Batis, p= 0.003
(c) Sarcocornia, p= 0.003
1.0
0.5
0.0
-0.5
-1.0
Relative interaction intensity (RII)
Observation
Plot
Transect
Transplant
Survey Method

Figure 7


(a) Observation Survey
2D Stress: 0.07
Mangrove
Marsh
NMDS2
NMDS1
2
1
0
-1
-2
(b) Plot Survey
2D Stress: 0.08
NMDS2
NMDS1
(c) Transect Survey
2D Stress: 0.09
NMDS2
NMDS1